*Habitat Description and Resource
Utilization: A Preliminary Report
on Mantled Howling Monkey Ecology*

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INTRODUCTION

In the past decade there has been an increasing awareness of the relationship between primate social organizations and their environments (Crook and Gartlan 1966; Denham 1971; Eisenberg et al. 1972). The literature to date contains many studies of primate social behavior, but the concomitant investigations of ecological parameters are absent. Eisenberg et al. (1972) have suggested that this "lack of sound ecological studies" prevents insight into the adaptiveness of primate social systems. True, almost every paper on primate behavior does contain a few paragraphs giving geographical location, rainfall, temperature extremes, etc., and a generalized description of habitat cover ("thorn scrub," "open savanna," "tropical wet forest," "evergreen seasonal forest") to describe the study site. But, unfortunately, even this cursory ecological information often is gathered incidentally to the behavioral study.

Conspicuous by its absence is detailed information about the natural diets of free-ranging primates in general and herbivorous primates in particular. I wish to thank Dr. Russell Tuttle for suggesting howlers as a research project and for his guidance and advice throughout the study. I am grateful to the Werner Hagnauers for allowing me to work on Hacienda La Pacifica. I also wish to express my appreciation to Dr. Paul Opler for identifying the trees and to Dr. Norman Scott for developing and implementing the capture and marking technique and for his help in the capture of my study group. In addition, thanks go to C. Opler, T. Opler, and B. Scott for their help in mapping the trees. J. Bradbury, R. Carroll, D. Janzen, P. Opler, and S. Vehrenkamp critically commented on the manuscript. The field work was supported in part by National Science Foundation Grant GS 31733.

particular. Often leaf-eating primates, such as howling monkeys (*Alouatta* spp.) are assumed to have an unlimited food supply and, therefore, not to be food limited (Carpenter 1934; Altmann 1959; Hladik et al. 1971). Observations of howlers dropping what appeared to be food (Carpenter 1934; Altmann 1959; Hladik et al. 1971) and leaving a tree before all of the apparent food was eaten (Carpenter 1934; Richard 1970) are given as evidence for an overabundance of available food.

The gathering of such fundamental information as (1) the natural diet of free-ranging primates, (2) the distribution of resources, and (3) the seasonality of resources can help provide the needed prerequisites for the correlations between environment and social structure. Indeed, is it better to specialize on a single resource or to feed on a wide variety of plant foods? What are the habitat similarities or differences which may be shaping various primate social systems? And, how might these ecological variables influence a primate's behavior?

This paper presents the results of the first six months of a twelve-month study aimed at providing a detailed description of the habitat as well as quantifying information on resource utilization by one group of mantled howling monkeys (*Alouatta palliata*) inhabiting a riparian forest in Costa Rica. Included in this report are 1365 hours of animal observation during 117 days from September 1, 1972, through March 2, 1973.

The Study Area

The study was conducted at Hacienda La Pacifica, Guanacaste Province, Costa Rica (10°28'N, 85°07'W). The ranch is 45 meters above sea level and is located in the Lowland Tropical Dry Forest life zone (Holdridge 1967). Most (92 percent) of the yearly average of rainfall (1,561 millimeters) falls between May and November, based on ten-year records (1960–1969) of the Servicio Meteorológico de Costa Rica. During the dry season, which extends from December through April, strong trade winds blow from the northeast. It is during this time that most of the trees in the dryland areas and some in the riparian forest drop their leaves and remain leafless for most of the dry season (Janzen 1967).

Approximately one-fourth of the ranch is in forest which has been disturbed in various degrees while the remainder has been cleared for farming. In clearing, total deforestation is not practiced; rather, wind-

break strips and riparian forests are often left to protect against wind and water erosion.

The study site consisted of narrow bands of riparian forest on the banks of the Río Corobici with wider strips of dry deciduous forest extending laterally into the fields on either side. The river strips were the width of a single tree in some places, about 60 meters wide at the widest point, and 640 meters in length. One of the dry forest strips was 30 meters wide by 170 meters long, and the other was 80 meters wide by 140 meters long. The study area could be divided into riparian and dry regions (these distinctions were based on the kinds, proportions, and phenologies of tree species present) with the river dividing the riparian forest, resulting in four distinct regions (Figure 1). There were cleared fields surrounding all of the range except to the northeast where the riparian forest continued upstream.

Figure 1. The study site as delimited by Group 1. Areas 1 and 4 are dry regions while Areas 2 and 3 are riparian

Group Composition

During the period of this report my study group (Group 1) consisted of two adult males, six adult females, and five juveniles. A juvenile is defined as an animal not carried by an adult but less than two years old (see Table 5 for names and weights).

Another group (Group 2) occasionally moved into the study area from upriver. It consisted of six adult males, sixteen adult females, twelve juveniles, and two infants. An infant is any animal that is carried continuously by an adult.

Methods

Because the primary concern of this study was to analyze the relationship between the habitat and the monkeys, the initial two months were devoted to obtaining detailed parameters on the environment. Each tree (a self-supporting woody plant more than four meters in height) within the study group's range was numbered consecutively, and tree heights, diameters, and canopy depths were measured. The trees were also identified as to species where possible.

One of the difficulties of observing arboreal animals is the problem of being able to see all, or even a few of the subjects. Other investigators have employed various observational methods in an effort to overcome the problems of visibility and the bias of individual animal observability intrinsic to the study of a free-ranging primate inhabiting forested areas (McClure 1964; Chalmers 1968; van Lawick-Goodall 1968; Beck and Tuttle 1972). Prior to this study I developed a method that I call Randomized Individual Observation (RIO) which was used successfully throughout this field work. RIO is based upon the strategy of continuously monitoring the behavior of one animal per day. A different subject animal may be observed each day or the same animal may be observed for several successive days. The order of individual observation is determined by a random digit table.

RIO is designed to eliminate any possible bias that the investigator may unintentionally introduce into the order of individual observations because of personal preference or the ease with which certain ages and/or sex classes may be observed. By concentrating on a single animal the observer is not distracted by the movements of other animals and can follow the subject animal for longer periods of time. There is then much less unproductive observation time which must be

filled with educated guesses. Using RIO, data can be collected on the duration of activities and time-energy budgets can be calculated.

Unambiguous recognition of each individual within the study group is an absolute necessity for the successful employment of RIO. To facilitate positive identification of the thirteen members of my study group, leather collars with metal tags of different colors were put around the necks of the six adult females. The adult males could be distinguished by physical characteristics. The juveniles were too small for collars and could be differentiated by their size and close association with a tagged female. To capture the animals, a controlled dose of Anectine (*Succinylcholine chloride*) was delivered by a CO₂ gun. A large piece of canvas, rigged with handles, was used to catch the animals as they fell from the trees.

Observations were usually begun about 0500 (on several days observations were begun at 0400) and terminated at 1800 or at sunset. Prior to 0500 I would place myself in position under the subject animal for the day, using a headlamp to verify the individual's identity. Howlers seldom move at night and are fairly easy to locate the next morning if their position for the previous night is known. During two all-night observations the animals being observed did not move at all other than to shift positions. On many mornings the subject animal was found in the same location in which it had been the preceding night. Occasionally animals changed branches but usually moved less than twenty-five feet and seldom changed trees. Although they did not move very much at night, Group 1 was observed traveling through the trees on several nights around midnight, and often began feeding well before dawn (as early as 0400) and continued feeding past sunset (as late as 1830). During this study sunrise occurred at about 0510 and sunset about 1755. Once located, the subject's position in relation to the positions of other animals in the tree was noted and the continuous monitoring of the subject's behavior was initiated.

The time of onset of any new activity and the activity were noted. If the activity was feeding, the tree number (for later species identification), location in the tree, feeding posture, and part of the tree eaten were recorded. An attempt at quantifying the amount eaten was made by counting mouthfuls, or in some instances, the number of fruits eaten, in order to determine relative importance of the various tree species. In quantifying the feeding data two stop-watches were used simultaneously. A record was also kept of the numbers of the trees through which the animals moved. This information will be used to view area utilization.

In order to compare the howlers' movements with food seasonality a weekly record was kept of the flowering, fruiting, and leaf production of the numbered trees.

RESULTS

During the first six months of the study the four areas of the study site, as delimited by the study group, contained a total of 1,348 trees representing ninety-two species from thirty-eight families (Table 1).

Table 1. A complete list of the tree species present in the study site. The species are arranged alphabetically by family with the common name in quotation marks and the number of individuals in parentheses. If the species is a food source, the part(s) of the tree used as food is listed. An asterisk indicates the species was utilized as a primary source of food. A # indicates a dioecious tree species

ANACARDIACEAE	
* <i>Anacardium excelsum</i> "Espavel" (68)	de chivo" (30)
new leaf petiole, pedicel, flowers, new leaves	flowers, flower buds
# <i>Astronium graveolens</i> "Ronron" (7)	<i>Tabebuia rosea</i> "Roble de sabana" (32)
flower buds, leaves	flowers, flower buds
<i>Mangifera indica</i> "Mango" (8)	BIXACEAE
green & ripe fruit	<i>Bixa orellana</i> "Achiote" (6)
# <i>Spondias mombin</i> "Jobo" (14)	BOMBACACEAE
fruit, leaf pulvillus, new leaves, leaves	<i>Bombacopsis quihada</i> "Pochote" (4)
# <i>Spondias nigrescens</i> (7)	leaves
leaf pulvillus, flower buds, fruit	<i>Ceciba pentandra</i> "Ceiba" (6)
<i>Spondias purpurea</i> "Yocote" (31)	<i>Ochroma lagopus</i> "Balsa" (1)
leaves	BORAGINACEAE
ANNONACEAE	<i>Bourreria quitroxi</i> (2)
<i>Annona holosericea</i> "Anona" (7)	flower buds, flowers
<i>Annona purpurea</i> "Soncoya" (3)	<i>Cordia alliodora</i> "Laurel" (39)
<i>Sapranthus palanga</i> "Palanca" (5)	leaves
APOCYNACEAE	# <i>Cordia collococca</i> (17)
<i>Rauwolfia</i> sp. (1)	leaves, flower buds
ARALIACEAE	<i>Cordia dentata</i> (194)
# <i>Scadodendron excelsum</i> "Jobo de lagarto" (1)	fruit
BIGNONIACEAE	# <i>Cordia panamensis</i> (5)
<i>Crescentia cujete</i> "Calabacero jicaro" (7)	BURSERACEAE
<i>Godmania ascutifolia</i> "Corteza de chivo" (23)	# <i>Bursera sinarubra</i> "Indio desnudo" (18)
<i>Tabebuia neochrysantha</i> "Corteza	new leaves, leaves
	CAESALPINIACEAE
	<i>Hymenaea courbaril</i> "Guapinol" (61)
	new leaves
	* <i>Schizolobium parahybum</i> "Galli-

Table 1 (continued)

nazo" (6)	new leaves, leaves, flowers
flowers, fruit	# <i>Trichilia</i> sp. (12)
<i>Cassia grandis</i> "Carao" (1)	MIMOSACEAE
CAPPARIDACEAE	<i>Albizia adinocephala</i> "Gavilana" (1)
<i>Caparis indica</i> (2)	new leaves
<i>Craeva tapia</i> (1)	<i>Albizia</i> sp. (2)
CARICACEAE	<i>Euteropium cyclocarpum</i>
# <i>Carica papaya</i> "Papaya" (1)	"Guinacaste" (13)
leaves	leaves, flower buds, flowers
<i>Stemmadenia obovata</i> (2)	* <i>Inga vera</i> var. <i>spuria</i> (3)
COCHLOSPERMACEAE	new leaves, flowers
<i>Cochlospermum vitifolium</i> "Poro-poro" (30)	<i>Lysitoma seemanii</i> "Quebracho" (22)
flower buds	* <i>Pithecellobium longifolium</i> "Sotocaballo" (16)
ELAEOCARPACEAE	new leaves, flowers
* <i>Muntingia calabura</i> "Capulin" (7)	* <i>Pithecellobium saman</i> "Cenicero" (10)
fruit, flowers, leaves	new leaves, leaves, flowers, fruit
* <i>Andira inermis</i> "Carne asada" (30)	MORACEAE
new leaves	<i>Brosimum costaricanum</i> "Ojoché" (1)
<i>Dalbergia retusa</i> "Cocobola" (11)	# <i>Cecropia peltata</i> "Guarumo" (4)
* <i>Gliricidia sepium</i> "Madera negra" (103)	leaf petiole, fruit, new leaves
leaves, new leaves, flowers, fruit	# <i>Chlorophora tinctoria</i> "Mora" (7)
<i>Lonchocarpus costaricensis</i> (6)	leaves
<i>Lonchocarpus hondurensis</i> (2)	* <i>Ficus</i> sp. "Higuera" (3)
flowers, fruit	new leaves
* <i>Lonchocarpus minimiflorus</i> "Chaperno" (66)	MYRTACEAE
flower buds, flowers	<i>Eugenia salmensis</i> (76)
* <i>Pterocarpus hayesi</i> "Sangre de drago" (4)	fruit
new leaves, leaves	<i>Ptilium guajava</i> "Guayaba" (1)
FLACOURTIACEAE	NYCTAGINACEAE
<i>Casaria aculeata</i> (7)	# <i>Pisonia nueranthiocarpa</i> "Petrone" (6)
<i>Casaria arborea</i> (6)	OLACACEAE
<i>Laetia thumia</i> (2)	<i>Schoepfia schreberi</i> (4)
# <i>Xylosma flexuosum</i> (2)	PAPILIONOIDEAE
HIPPOCRATACEAE	* <i>Myrospermum frutescens</i> (13)
<i>Hemilingium excelsum</i> (9)	leaves, new leaves, flowers
LAURACEAE	PIPERACEAE
<i>Ocotea veraguensis</i> (1)	<i>Piper tuberculatum</i> (1)
MALPIGHIACEAE	leaves
<i>Byrsotoma crassifolia</i> "Nance" (2)	POLYGONACEAE
MELIACEAE	# <i>Coccoloba caracasana</i> "Papaturro blanco" (9)
<i>Cedrela mexicana</i> "Cedro amargo" (5)	new leaves
# <i>Guarea luxii</i> (13)	ROSACEAE
new leaves	* <i>Licania arborea</i> "Alcornoque" (29)
<i>Swietenia humilis</i> "Caobo" (11)	new leaves, flower buds
# <i>Trichilia cuneata</i> (5)	

Table 1 (continued)

RUBIACEAE	
<i>Calycohyllum candidissimum</i>	flower buds, flowers, fruit
"Madrona" (17)	
leaves	
<i>Chomelia spinosa</i> (3)	
leaves	
# <i>Genipa caruto</i> "Guazitel" (2)	
<i>Guettarda macroperma</i> (2)	
leaves	
RUTACEAE	
<i>Citrus limeta</i> "Lima dulce" (1)	
# <i>Zanthoxylum procerrum</i> (4)	
leaves, new leaves	
SAPINDACEAE	
<i>Thouinidium decandrum</i> (16)	
SAPOTACEAE	
* <i>Manilkara achras</i> (6)	
fruit	
* <i>Mastichodendron tempsique</i> (6)	
SIMAROUBACEAE	
# <i>Picramnia latifolia</i> (1)	
# <i>Simarouba glauca</i> "Olimo" (7)	
leaves, fruit	
STERCULIACEAE	
<i>Guazuma tomentosa</i> "Guacimo" (185)	
new leaves	
<i>Sterculia apetala</i> "Panama" (3)	
TILIACEAE	
<i>Apeiba tibourbou</i> "Peine de mico" (4)	
<i>Luehea candida</i> "Guacimo macho" (54)	
new leaves	
<i>Luehea speciosa</i> "Guacimo molentillo" (4)	
flower buds, flowers	

There are fifteen species (16 percent) represented by only one individual while the most numerous tree species, *Cordia dentata*, numbered 194. In this particular life zone a riparian habitat can be defined by the presence of *Anacardium excelsum* and *Platycodon longifolium*. There are twenty (22 percent) dioecious tree species in the study site. These twenty species include 10 percent of the total number of individuals (134 of 1,348). Dioeciousness of a species affects the monkeys by reducing the number of individuals which provide fruit because only the female trees produce fruit. Of such species Group 1 fed on the fruit of *Cecropia peltata* (one female of four individuals), *Spondias mombin* (six females of fourteen individuals), *Spondias nigrescens* (four females of seven individuals), and *Chlorophora inctoria* (four females of seven individuals).

Two of the species found in my study site are not indigenous to this area, i.e. *Mangifera indica* and *Citrus limeta*. *M. indica* is used as an occasional food source.

Group 1 spent two days feeding in Area 1, seven days feeding in Area 4, and the remaining 108 days feeding along the river, with sixty-four days in Area 2 and forty-four days in Area 3. The visits to Area 1 were to feed on *Manilkara achras* and *Mastichodendron tempsique* flower buds and flowers. The seven days spent in Area 4 were all during the *Cordia dentata* fruiting season. During the dry season the trees of these two areas (except *Hymenaea courbaril*) dropped their leaves

and remained bare while the riparian area species were flowering, fruiting, and producing new leaves.

The howler's movements throughout the range appeared to be coordinated with the trees' phenology. For example, in several instances the group moved from one side of the river to the other when individuals of *Platycodon longifolium* on the opposite river bank began to produce new leaves. Often new leaves, fruit, flowers, and buds are a bright color and visible for long distances against the backdrop of green leaves or brown branches. Possibly the odor of the fruit also caused howlers to determine that a move would be rewarded. Because the group moved through its range quite frequently, it also might have been obtaining direct cues of events which would occur in the near future, such as flowering or new leaf production.

At first glance Group 1 appeared to be generalists because they utilized 54 percent (fifty of ninety-two) of the species available to them. But when only the species primarily used as resources by Group 1 were considered, they were shown to be much more selective in their food choice. Only 23 percent (twenty-one of ninety-two) of the total species available to Group 1 were used as primary resources. A primary resource is defined as one which has been utilized as a food source more than seven times.

Many of the fifty species were utilized by Group 1 only once or twice. For example, one of the adult males was observed to feed on leaves of *Carica papaya* for less than three minutes on a single occasion; an adult female took only two bites of new leaves from a single *Guazuma tomentosa*; and once a juvenile and adult female were seen to feed briefly on leaves of a *Bombacopsis guianensis*. Other species not noted with an asterisk in Table 1 were utilized more frequently than those mentioned above, but not as regularly as the primary resources. The howlers may have had limited access to the food item because of the seasonality of the food, or possibly they may have been using that particular resource at the time to balance their diet or because something else which might have been preferred was not available. It is probable that some of these species which are not primary food sources at this time may become primary sources of food as the trees change seasonally.

Also, it may be that these trees contained substances which in higher concentrations were toxic to the monkeys but could be tolerated when eaten in smaller amounts. Certain ruminant artiodactyls can eat small amounts of toxic plant substances (Pearson 1965) and squirrels ingest small amounts of seeds containing canavanine which in large amounts

is probably toxic (Janzen 1971a). Many tropical plants have high concentrations of "secondary compounds" in their seeds or foliage which may be toxic to the plants' predators (Janzen 1970, 1971b). For example, *Gliricidia sepium* is called mata-raton (mouse killer) in Puerto Rico: the toxic seeds, bark, leaves, and roots are used to kill rats and mice (Little and Wadsworth 1964). There were 103 *G. sepium* individual trees present in the study site. Group 1 fed on the flowers of eighteen of the 103 individuals and only on the mature leaves, new leaves, and fruit of four of the 103 individual trees, two of which were located in Area 2 and two of which were located in Area 3. The foliage of these four trees may have had a lower toxin content.

Most of the food sources of the study group were contained in five families (Anacardiaceae, Fabaceae, Mimosaceae, Moraceae, Sapotaceae). New leaves of *Anacardium excelsum* and *Andira inermis* were eaten but not the mature leaves. The family Anacardiaceae contains a resinous exudate which can be very caustic. Some people cannot eat mango fruit because of this resin. *A. excelsum* produced a very large fruit crop per tree but the monkeys only ate the small fleshy stalk (pedicel), probably due to toxins in the fruit itself which were not present in the pedicel. The shell of the related *Anacardium occidentale* fruit contains a poisonous oil: cardol oil (Little and Wadsworth 1964). The family Moraceae probably also contains toxic secondary compounds because the howlers fed only on new leaves of *Ficus* sp. as well as the new leaves and the leaf petioles of new and mature leaves of *Cecropia peltata* plus the fruit of each of these species. *C. peltata* has an ant species which inhabits the hollow areas of the trunk and patrols the leaves and fruit. The ant may serve as an effective deterrent against some invertebrate and vertebrate predators.

The two families, Mimosaceae and Sapotaceae, are somewhat less sharply defined as to presence or absence of toxic compounds. Only the fruit and flowers of *Manilkara achras* and *Mastichodendron tempisque* were eaten. The fruit, flowers, new leaves, and mature leaves of *Pithecellobium saman* were eaten while mature leaves and fruit of *Pithecellobium longifolium* were not eaten but the new leaves were actively sought by Group 1.

Coriaria dentata fruit were available for only two weeks, but during that time the fruit represented a major part of the daily food intake as judged by the amount of time spent feeding. *Muntingia calabura* produced flowers, fruit, and leaves throughout the year and, although it comprised a very low percentage of the feeding time for any day, it was available every day. Probably the limiting factor in *M. calabura* use as

a food source was its location in the range and the availability of other resources. If the group passed through any *M. calabura* trees they almost always fed in them during the dry season, but they did not make special detours just to feed in *M. calabura* and utilized only two trees (both in the southern part of Area 3) of the seven trees in the range, probably because the other five were not located in areas frequently visited by the group members (all five were located in the northwestern part of Area 3). Utilization of *M. calabura* decreased to almost zero during the wet season.

During the time *Andira inermis* produced new leaves it served as a major daily food source. The twenty-one *A. inermis* on the east side of the river produced new leaves first and for ten days served as Group 1's major food source. As the leaves of the individuals on the east side of the river began to mature the group moved to the west side where the other *A. inermis* were then beginning to produce new leaves.

Some species provided the study group with more than one type of food, e.g. *Anacardium excelsum*. The howlers ate the very new leaves (less than two inches long), new leaf petioles, flower buds, flowers, and the fleshy fruit pedicels. Because *A. excelsum* began to flower, produce new leaves, and fruit at the end of the wet season and continued this production into the dry season, it was one of the major sources of food during the dry season. Another species which provided more than one type of food and was an important food source during the dry season as well as throughout the year was *Pithecellobium saman*. The howlers fed on mature leaves during both the wet and dry season and also fed on the new leaves which were produced in October and March. The fruits of *P. saman* were also eaten during the dry season just before they began to mature. The fruit, in earlier stages of development, also was eaten during the rest of the year because it takes one year from the time of pollination for the fruit to mature. Flowers usually occur in March and April and were also sought by Group 1. Because of an extremely dry wet season this past year, some of the *P. saman* individuals in the drier areas produced a crop of flowers during October and November, 1972.

The fruits of *Spondias mombin* and *Eugenia salamensis* were important food sources for Group 1. Both of these fruits were taken from the trees by mouth and swallowed after being briefly chewed. The adults were seen to tilt their heads back when chewing *S. mombin* fruits, which are very juicy, thus swallowing as much of the juice as possible. Apparently the monkeys select the fruit of *S. mombin* by color from a distance, for upon entering a fruiting tree they would look

around before moving to a certain area. They then appeared to accept or reject a particular fruit by odor, sniffing each one before eating it.

From the monkey's viewpoint, the year just past was not a good one in regard to the quantity of *E. salamensis* fruit. Of the seventy-six trees in the range, only four produced fruit. Possibly a lack of rain at a critical time resulted in the small fruit crop, or *E. salamensis* may produce a fruit crop every other year.

Feeding Postures

Although howlers have a prehensile tail and may use it in feeding, my study group often fed in the sitting or standing posture. Juveniles seemed to spend more of their feeding time hanging. Adults appeared to adapt their feeding posture to the conditions required to feed (Table 2). Three important determinants of whether sitting or hanging was used were the shape of the tree, the kind of food eaten, and the location of the food in the tree. If the food ingested was in a tree with a narrow, confined canopy, the food was likely to be in an upright position and could be reached by sitting in adjacent branches. If the tree had a wide spreading canopy the lower one-half of the canopy was usually either horizontal or arched toward the ground and the food could only be reached by hanging from the same branch or a branch above the food. Any food located in the upper half of this type of tree was likely to be positioned above the branch and could be reached by sitting on the branch. Normally most fruit hung below the level of a branch and could only be reached by hanging. This was especially true of large fruit of *Mangifera indica*, *Spondias mombin*, and *Eugenia salmensis*. *Cordia denata* fruit are borne in a cluster which projects upward and were usually eaten while sitting on adjacent branches.

Size difference was probably the main reason for juveniles hanging more than adults while feeding. Because they weighed less (three to five pounds as compared to ten to eleven pounds) they could get out to the ends of very small branches which bent under their weight, making it almost impossible to reach any food other than that lower down. However, if these terminal branches were upright, i.e. in the upper center of the tree, the juvenile like the adult was more likely to feed sitting. In trees such as *Pithecellobium saman* and *Ficus* sp. adults often spent their entire feeding time of fifteen to thirty-five minutes sitting. As yet there does not appear to be any individual preference by any member of Group 1 for either sitting or hanging.

Often while feeding in the sitting posture the tail was wrapped around an adjacent branch. Though it did not support any weight, it probably acted as a safety device against any sudden movement by other monkeys in the immediate vicinity or a strong gust of wind which can occur suddenly in the dry season. In certain situations the tail was used as a counterweight to offset the weight of the animal balanced on top of a branch while reaching out toward some nearby food. In these instances the tail was not anchored but was held free.

Feeding Rates

Part of the time spent in a resource tree by the monkeys was spent foraging for food. Foraging is defined as the time spent in a food tree either visually searching for food or moving from place to place within the tree. Foraging and feeding times appeared to depend upon the species used as a food tree. There was very little foraging time in *Licania arborea* when feeding on leaves, while 50 percent of the time was spent foraging in *Anacardium excelsum* when feeding on "pedicels" (Table 2). The number of pedicels eaten per unit time was a result of the number of fruit available in a tree (Table 3).

Mouthfuls of leaves per minute were counted in an effort to get an idea of the feeding rate and the amount ingested. Hladik et al. (1971) counted the number of leaves and then weighed a sample of the same species to determine the weight of food ingested. They estimated that an adult weighing 17.6 pounds ingested forty-two ounces of food. I took twenty-two ounces of mash from the caecum of a dead howler weighing eight pounds. This monkey's stomach was completely empty.

Drinking

Several members of Group 1 were seen to drink water from cisterns formed at the base of several branches or from holes in large branches. In all cases rain water had gathered in these areas, and the howlers hung by their tails with their heads down and inserted their heads into the opening. None of the members of Group 1 were seen to drink from the river, even though many of the trees had branches which touched the water. During the dry season the howlers apparently got all of the moisture they required from their food as the waterholes in the trees dried up from lack of rain.

The howlers did remove a large number of green fruit while feeding upon the pedicels of *A. excelsum* fruit, perhaps up to 10 percent of the trees' fruit crops, thereby lowering the number of fruit which reached maturity. The green fruit was picked from the trees with the mouth, grasped with either hand, the pedicel bitten off, and the fruit dropped.

DISCUSSION

Although my study group fed on 54 percent of the available tree species, only 23 percent of the total available tree species can be considered to be important or primary food sources. The twenty-one tree

Table 4. Utilization of the primary food species by Group 1

Tree species	Individual trees			Months during which tree species served as food and food type selected				
	# pres.	# used	% used	Sep.	Oct.	Nov.	Dec.	Jan. Feb.
<i>Anacardium excelsum</i>	68	45	66		NL	NLPE	NLPE	NLPE FRST
<i>Andira inermis</i>	30	19	63		NL	NL	NL	NL
<i>Bursera simaruba</i>	18	5	27		FR	PE	PE	NL
<i>Cecropia peltata</i>	4	3	75		FR	PE	PE	NL
<i>Eugenia salamensis</i>	76	3	3		FR	FR	FR	NL
<i>Ficus</i> sp.	3	3	100		NL	NL	NL	NL
<i>Gliricidia sepium</i>	103	18	17		LE	LE	LE	FL
<i>Inga vera</i> var. <i>spuria</i>	3	2	67		NL	NL	FL	NL
<i>Licania arborea</i>	29	15	50		NL	NL	NL	NL
<i>Lonchocarpus</i>								
<i>mhiniiflorus</i>	66	15	23		FL	FL	FR	FR
<i>Manilkara achras</i>	6	5	83		FR	FR	FR	FR
<i>Mastichodendron</i>								
<i>tempisque</i>	6	5	83		FBFL			FBFL
<i>Muntingia calabura</i>	7	2	28			LE	LE	FR
<i>Myrsine frutescens</i>	13	1	7		LE	LE	LE	FBFL
<i>Pithecellobium</i>								
<i>longifolium</i>	16	12	75		NL	NL	NL	NL
<i>Pithecellobium saman</i>	10	8	80		LENL	NLFL	LEFL	LE
<i>Pterocarpus hayesii</i>	4	2	50		NL	NL	NL	NL
<i>Schizolobium parahybnum</i>	6	5	83					FL
<i>Spondias mombin</i>	14	5	36		FR	FR	FR	PU
<i>Spondias nigrescens</i>	7	7	100		FR	FR	FR	PU
<i>Trichilia cuneata</i>	5	5	100		LE	LE	LE	LE
NL	= new leaves							
NLPE	= new leaf petiole							
FRST	= fruit stalk (petiole)							
LENL	= leaves and new leaves							
FR	= fruit							
PE	= leaf petiole							
LE	= leaves							
FBFL	= flowers and flower buds							
NLFL	= new leaves and flowers							
LEFL	= leaves and flowers							
LEFR	= leaves and fruit							
FRPU	= fruit pulvinus							
PU	= pulvinus							
FL	= flowers							

Table 5. Composition of my study group for the six months of this report

Animal	Sex	Date	Weight	Mother	Comments
Scar	male	6/22/73	13 lb. 12 oz.	—	—
Baker	male	6/19/73	15 lb. 6 oz.	—	—
White/red	female	6/22/73	9 lb. 1 oz.	—	—
Blue	female	6/19/73	11 lb. 6 oz.	—	—
Yellow	female	6/19/73	10 lb. 3 oz.	—	—
Green	female	6/19/73	10 lb. 11 oz.	—	—
Green/red	female	6/19/73	11 lb. 8 oz.	—	—
Dogcollar	female	8/16/72	11 lb. 3 oz.	—	—
Charlie	male	6/22/73	8 lb. 2 oz.	Yellow	—
Able	male	3/25/73	5 lb. 4 oz.	White/red	—
Bonnie	female	1/12/73	4 lb. 5 oz.	Dogcollar	—
Shadow	male	—	—	Blue	—
Infant	male	—	—	Blue	Disappeared 1/20/73

species classed as primary food sources contained 53 percent (709 of 1,348) of all the trees in Group 1's range (Table 4). However, this is not an accurate picture of the overall selectivity of Group 1. They utilized only 257 individual trees of the 1,348 trees available to them in their range. In addition, Group 1 did not feed on all individuals of a tree species in its range, but in most cases on only a select few. An extreme example of this selectivity was demonstrated by Group 1 feeding on the mature leaves of only four of the 103 individuals of *Gliricidia sepium* present in the range. Possibly these figures represent the number of individuals required to provide all of the nutrients the howlers needed. If we can assume that all individuals of a tree species contain similar nutrients, then the monkeys should feed equally on all of the individual trees within a food species. In the same manner, if it can be assumed that all species of trees can be utilized as food sources, howlers should be expected to demonstrate little selectivity between tree species in their choice of food, or at most only demonstrate individual peculiarities. Such is not the case for my study group. Rather, the monkeys returned to the same individual trees and fed selectively on certain species, certain individual trees, and selected parts of those trees at certain seasonal stages.

This selectivity within a food species (e.g. *Gliricidia sepium* with four of 103) as well as between species (twenty-one of ninety-two) may be the result of secondary substances produced by the trees as a deterrent to herbivores thereby narrowing the feeding niche of the howler. In opposition to this restriction is the howler's need to meet nutritional demands. The sampling of more tree species (fifty of ninety-two) may indicate that it is highly advantageous for howlers to maintain a suf-

ficiently diverse gut flora and fauna in order to survive even a slight perturbation of the available resources (Janzen, personal communication).

The secondary substances which the plants have evolved as defenses against herbivores may be of critical importance both to the individual animal and to group social behavior. The action of these plant toxins may be direct as demonstrated by the rat poison made from the bark and leaves of *Girardinia sepium*. Or, it may be indirect in the manner of tannins, as found in mature oak leaves, which bind proteins into indigestible complexes (Feeny 1970). An even more indirect effect of the plant toxins might be the subtle interference with the animals' reproductive cycles, such as occurs in insects (Ellis et al. 1965).

Plant secondary substances may have played an important role in primate evolution. The presence of intestinal flora may permit herbivores to ingest a diet high in secondary substances which would be toxic to them without the gut flora to detoxify the toxins, e.g. rodents living on a high oxalate diet (Shirley and Schmidt-Nielsen 1967). Possibly the protection offered by the intestinal flora allowed herbivorous primates to invade an ecological niche not available to animals without such an adaptive mechanism. Because caffeine and nicotine are alkaloids (Whittaker and Feeny 1971) man's ability to tolerate many toxins in his food and his use of plant-derived stimulants and hallucinogenics may be a legacy of his herbivorous ancestors.

The suggestion of an unlimited food supply for a herbivore, such as the howler, implies an animal which can use a wide variety of available plant food and which has evolved the ability to detoxify a broad range of toxic materials found in these foods. The detoxification of a wide range of plant foods containing many different toxic compounds requires the herbivore to expend a majority of its energy and nutrients to maintain the detoxification mechanisms necessary to handle this variety of toxins (Whittaker and Feeny 1971). Prior to the present fieldwork previous investigators concluded that the range of a howler group contained more food than the group would ever be able to utilize, and that food availability played no part in limiting the population density (Carpenter 1934; Altmann 1959; Chivers 1969; Hladik et al 1971). They would probably agree with Hairston, Smith, and Slobodkin (1960) that herbivores are not limited by the available food, but by other factors, such as disease and predators, which keep their number from increasing until all the food is eaten. In viewing the relationship between the howlers and the potential food available in their habitat, I would propose that the idea first suggested by Stahl in

1888 (Fraenkel 1959), "that not all that is green is palatable," be considered before *a priori* conclusions as to the quantity or quality of available food are made.

My study group utilized only a fraction of the tree species available in their range, only certain individuals of some food species, and less than 20 percent of the total number of trees present in their range. Their lack of activity may be the price howlers pay, in terms of maintaining their detoxification system, for feeding on the particular tree species which meet their nutritional requirements. It seems highly unlikely that the howler can maintain a detoxification system necessary to meet the added demands that ingestion of all available resources would place upon their digestive systems.

An apparent independence of free water during the dry season can be related to a finding of Feeny (1970) that the water content of immature leaves is higher than mature leaves. Many of the riparian trees, which are primary food species, produce new leaves during the dry season. Therefore, it is very likely that the howlers acquire sufficient water from their food and do not need to drink from the river.

Hladik et al. (1971) suggest that an exclusive fruit diet would be deficient in proteins. Indeed, even on those days when fruit made up most of the daily intake of food, Group 1 always ingested some leaves, possibly, as Hladik et al. (1971) have suggested, to balance the diet. It is this need for a balanced diet which may explain why howlers leave a tree before the available food is depleted. Also, departure may indicate that the howlers have ingested as much of that food as they can detoxify. To the degree that contemporary studies can elucidate the ecology and behavior of early hominids, detailed information on the diet of extant primates may be important. Fossil evidence of plants or of pollen are sometimes available from the area which a fossil primate probably inhabited. Knowing the relationship between an extant primate and its habitat can provide an insight into some of the selection pressures which may have acted on the extinct primates, such as a gradual change in climate which resulted in an alteration in the composition of tree species and thus in the primates' resources.

REFERENCES

- ALTMANN, S. A.
1959 Field observations on a howling monkey society. *Journal of Mammalogy* 40:317-330.

- BECK, B. B., R. TUTTLE
1972 "The behavior of gray langurs at a Ceylonese waterhole," in *The functional and evolutionary biology of primates*. Edited by R. Tuttle, 351-377. Chicago: Aldine.
- BERNSTEIN, I. S.
1964 A field study of the activities of howler monkeys. *Animal Behavior* 12:92-97.
- CARPENTER, C. R.
1934 A field study of the behavior and social relations of howling monkeys (*Alouatta palliata*). *Comparative Psychology Monographs* 10:1-68.
- CHALMERS, N. R.
1968 Group composition, ecology, and daily activities of free-living mangabays in Uganda. *Folia Primatologica* 8:247-262.
- CHIVERS, D. J.
1969 On the daily behavior and spacing of howling monkey groups. *Folia Primatologica* 10:48-102.
- COLLIAS, N. E., C. SOUTHWICK
1952 A field study of population density and social organization in howling monkeys. *Proceedings of the American Philosophical Society* 96:143-156.
- CROOK, J. H., J. S. GARTLAN
1966 Evolution of primate societies. *Nature* 210:1200-1203.
- DENHAM, W. W.
1971 Energy relations and some basic properties of primate social organization. *American Anthropology* 73:77-95.
- EISENBERG, J. F., N. A. MUCHENHORN, R. RUDRAN
1972 The relation between ecology and social structure in primates. *Science* 176:863-874.
- ELLIS, P. E., D. B. CARLISLE, D. J. OSBORNE
1965 Desert locusts: sexual maturation delayed by feeding on senescent vegetation. *Science* 149:546-547.
- FEENEY, P. P.
1970 Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51:565-580.
- FRAENKEL, G. S.
1959 The raison d'être of secondary plant substances. *Science* 129:1466-1470.
- HAIRSTON, N. G., F. E. SMITH, L. B. SLOBODKIN
1960 Community structure, population control, and competition. *American Naturalist* 94:421-425.
- HLADIK, C. M., A. HLADIK, J. BOUSSET, P. VALDEBOUZE, G. VIROBEN, J. DELORT-LAVAL
1971 Le régime alimentaire des primates de l'île de Barro Colorado (Panama). *Folia Primatologica* 16:85-122.
- HOLDRIDGE, L. R.
1967 *Life zone ecology*. San Jose, Costa Rica: Tropical Science Center.

- JANZEN, D. H.
1967 Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* 21:620-637.
- 1970 Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501-528.
- 1971a Escape of juvenile *Dioclea megacarpa* (Leguminosae) vines from predators in a deciduous tropical forest. *American Naturalist* 105:97-112.
- 1971b Seed predation by animals. *Annual Review of Ecology and Systematics* 2:465-492.
- JOLLY, A.
1972 *The evolution of primate behavior*. New York: Macmillan.
- KENOYER, L. A.
1929 General and successional ecology of the lower tropical rain-forest at Barro Colorado Island, Panama. *Ecology* 10:201-222.
- LITTLE, E. L., JR., F. H. WADSWORTH
1964 *Common trees of Puerto Rico and the Virgin Islands*. Washington, D.C.: U.S. Department of Agriculture.
- MC CLURE, H. E.
1964 Some observations of primates in climax diptocarp forest near Kuala Lumpur, Malaya. *Primates* 5:39-58.
- NEVILLE, M. K.
1972 The population structure of red howler monkeys (*Alouatta seniculus*) in Trinidad and Venezuela. *Folia Primatologica* 17:56-86.
- PEARSON, H. A.
1965 Rumen organisms in white-tailed deer from south Texas. *Journal of Wildlife Management* 29:493-496.
- POPE, B. L.
1966 The population characteristics of howler monkeys (*Alouatta caraya*) in Northern Argentina. *American Journal of Physical Anthropology* 24:361-370.
- RACENIS, J.
1952 Some observations on the red howling monkey (*Alouatta seniculus*) in Venezuela. *Journal of Mammalogy* 33:114-115.
- RICHARD, A.
1970 A comparative study of the activity patterns and behavior of *Alouatta villosa* and *Ateles geoffroyi*. *Folia Primatologica* 12:241-263.
- SHIRLEY, E. K., K. SCHMIDT-NIELSEN
1967 Oxalate metabolism in the pack rat, sand rat, hamster, and white rat. *Journal of Nutrition* 91:496-502.
- VAN LAWICK-GOODALL, J.
1968 The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs* 1(3):161-311.
- WHITTAKER, R. H., P. P. FEENEY
1971 Allochemics: chemical interactions between species. *Science* 171:757-770.